

## Light quantity and quality on the forest floor of pioneer and climax stages in a birch – beech – sugar maple stand

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The quantity and quality of solar radiation (300 to 1100 nm) beneath forest canopies were compared on sunny (sunflecks excluded) and cloudy days between the pioneer and climax stages of a birch – beech – sugar maple stand, and among the main species within these two stages of succession. The climax stage (mature canopies) transmits less energy between 300 and 1100 nm and casts smaller red to far red ratios than the pioneer stage (5-year-old canopies) on both sunny and cloudy days. Moreover, the canopies of the main species within each of these two stages of succession do not transmit the same quantity and quality of solar radiation. All these differences are greater on cloudy than sunny days. Leaf transmittance varies among species but this alone does not explain the differences in canopy transmission among these same species. The results are discussed in relation to the ecological significance for the plants growing under birch – beech – sugar maple stands.

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La quantité et qualité du rayonnement solaire (300 à 1100 nm) sous couvert forestier ont été comparées en journées nuageuses et ensoleillées (en évitant les taches de lumière) entre le stade pionnier et climacique d'une érablière à bouleau jaune et hêtre à grandes feuilles, ainsi qu'entre les principales espèces qui composent ces deux stades de succession. Le stade climacique (couverts forestiers matures) transmet moins d'énergie entre 300 et 1100 nm et induit un rapport rouge clair : rouge sombre plus faible que le stade pionnier (couverts forestiers de 5 ans) et cela autant en journées nuageuses qu'ensoleillées. De plus, il existe des différences dans la quantité et qualité du rayonnement solaire transmis au sol entre les principales espèces qui composent chacun de ces deux stades de succession. Toutes ces différences sont plus marquées en journées nuageuses qu'ensoleillées. Les facteurs de transmission des feuilles varient entre les espèces, mais ces différences n'expliquent pas à elles seules les différences de transmission mesurées au sol entre les différentes espèces. Les auteurs discutent des résultats en relation de leurs importances écologiques pour les plantes croissant sous l'érablière à bouleau jaune et hêtre à grandes feuilles.

### Introduction

Forest canopies significantly alter both the quantity and the quality of incident solar radiation reaching the understory. The alterations are a function of thickness (Reifsnyder and Lull 1965) and structure of the canopy (Alukova *et al.* 1964), spectral properties of leaves, solar elevation, and sky conditions (Floyd *et al.* 1978). Broadleaf deciduous canopies, for example, act as a filter, which transmits less energy in the ultraviolet and PAR (photosynthetically active radiations, 400–700 nm) than in the far-red and near infrared spectral regions, and also transmits less energy in the blue and red than in the green spectral regions (Vézina and Boulter 1966; Federer and Tanner 1966; Goodfellow and Barkham 1974).

Although we know that forest canopies alter the quantity and quality of solar radiation reaching the forest floor, few attempts have been made to evaluate variations occurring between and within forest stands. Federer and Tanner (1966) and Vézina and Boulter (1966) have shown that deciduous canopies are more selective in transmitting PAR than coniferous canopies: coniferous canopies partition the various components of shortwave radiation (direct and indirect, reflected and scattered, sunlight and sky light) reaching the forest floor differently than deciduous canopies (Reifsnyder

*et al.* 1971). Freyman (1968) has shown that the quantity and quality of solar radiation (400–750 nm) reaching the forest floor can differ among trembling aspen (*Populus tremuloides* Michx.), lodgepole pine (*Pinus contorta* Dougl.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Within any stand the proportion of infrared radiation increases with canopy density (Stoutjesdijk 1972a; Goodfellow and Barkham 1974; François *et al.* 1985). In mature canopies, Floyd *et al.* (1978) reported that as the foliage of a mixed oak (*Quercus alba* and *Quercus rubra* L.) and yellow-poplar (*Liriodendron tulipifera* L.) canopy develops, the spectrum becomes richer at 550 nm (green) compared with either 450 nm (blue) or 625 nm (red).

More recently, three studies have looked specifically at the changes in PAR and red to far red (R:FR) ratios under different coniferous and deciduous canopies. Morgan *et al.* (1985) did not find any difference in the R:FR ratio between two *Pinus radiata* stands of different stocking (medium (750 trees/ha) vs. high (6700 trees/ha)) but of similar leaf area indices. Hughes *et al.* (1985) found that following leaf emergence there was first a rapid decrease in PAR and R:FR ratio under an oak canopy, and little change afterward throughout the summer. Also, they did not find any evidence of increasing canopy transmittance on cloudy days compared with sunny days. This latter result contradicts previous reports by Federer and Tanner (1966) and Vézina and Boulter (1966). Finally, Ross *et al.* (1986) showed that PAR and R:FR ratios varied between early and late successional coniferous forest ecosystems of central Alberta.

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TABLE 1. Characteristics of the birch - beech - sugar maple stand studied during July 1985

Age	Density (no./ha) <sup>a</sup>	Species	Height (m)	Crown coverage (% of stand) <sup>b</sup>
Pioneer stage, 4- to 5-year-old species	10 000 – 35 000	Pin cherry	1.5–2.5	45
		Raspberry	0.3–1.0	20
		Mountain maple	1.0–2.0	10
		Red maple	1.0–3.0	10
		Yellow birch	0.5–1.0	5
		Sugar maple	0.5–0.8	3
		Striped maple	1.0–2.0	3
		American beech	0.3–0.8	2
		American elder	0.8–1.5	1
Mature or climax stage, 80- to 185-year-old species	200–500	Sugar maple	15–20	45
		American beech	14–18	25
		Yellow birch	12–17	20
		Others	—	<5

<sup>a</sup>Trees taller than 0.3 m for the pioneer stage and stems >5 cm at 1.4 m above the ground for the climax stage.

<sup>b</sup>Estimated by projecting the crown area of each tree on the forest floor.

This recent interest in investigating the R:FR ratio as well as the PAR under different forest canopies is largely due, as stated by the authors of these three recent studies cited above, to the increasing evidence that the variations in R:FR ratio induced by forest canopies are detected by plants through the pigment phytochrome. Phytochrome has two forms,  $P_r$  and  $P_{fr}$ , with absorbance peaks in the red (660 nm) and far-red (730 nm) wavelengths, respectively (Smith 1982). The equilibrium between the  $P_r$  and the  $P_{fr}$  forms depends on the relative proportions of light in red and far-red wave bands. Moreover, there is some evidence that plants may detect variations in light quantity through another pigment (blue absorbing photoreceptor (BAP) or cryptochrome) acting in the 300-500 nm wave bands (Smith 1982).

The perception of the variations in the light environment has crucial ecological implications for plant growth. It has been shown, in effect, that different herbaceous and agricultural plants (Holmes and Smith 1975; Morgan and Smith 1981; Hoddinott and Hall 1982; Holmes *et al.* 1982; Corre 1983; and many others), *Pinus thunbergii* and *Betula platyphylla* var. *japonica* (Morikawa and Asakawa 1976), *Pinus radiata* (Morgan *et al.* 1983), and two West African tree species, *Khaya senegalensis* and *Terminalia worrensis* (Kwesiga and Grace 1986), modified their pattern of growth under both different light qualities (R:FR ratio) and quantities (e.g., PAR). Moreover, light quantity and quality act on two very important plant processes, photosynthesis (Hoddinott and Hall 1982; Kwesiga *et al.* 1986) and germination (Bormann 1983; Bliss and Smith 1985). Therefore, considering the regulatory effects of both light quantity and quality on plant growth and development, it appears important to evaluate these two light components under different forest canopies. Only such an evaluation will enable us to fully understand the role of different light environments on the success or failure of plants growing in the understory.

Our objectives were to compare quantitatively (i) the radiant environment between 300 and 1100 nm beneath birch - beech - sugar maple stands in early and late successional stages on sunny and cloudy days, (ii) the spectral

transmission of the canopy of the main species found in both stages on sunny and cloudy days, and (iii) the leaf transmittance of these main species. The rationale for this final objective stems from the need to know whether or not the expected differences in the leaf transmittance of leaves among species constitute a major factor in explaining the differences in the quantity and quality of light measured under these same species. Furthermore, as far as we know there has been no study conducted to compare the quantity and quality of light under different species, and under the early and late successional stages of a deciduous stand.

### Materials and methods

The study area was located in the Duchesnay Experimental Forest, near Québec (71°40' W and 46°55' N), in a birch - beech - sugar maple stand. The mean annual precipitation is 122 cm, with a mean July temperature of 17.9°C. Measurements were taken *in situ* within three 50-m strips of both undisturbed old-growth birch - beech - sugar maple stands (climax stage) and alternating young stands clear-cut 5 years before (pioneer stage) on a western exposure. The overstory of the climax stage consisted of sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britton), whereas the overstory of the pioneer stage consisted of pin cherry (*Prunus pensylvanica* L.f.), raspberry (*Rubus* spp.), mountain maple (*Acer spicatum* Lam.), red maple (*Acer rubrum* L.), yellow birch, sugar maple, striped maple (*Acer pensylvanicum* L.), American beech, and American elder (*Sambucus canadensis* L.) (Table 1). Raspberry was present in the 5-year-old stand only where the main cover was absent or very open. In Table 1, the percentage of the entire crown covered by each species (i.e., crown coverage for each species) was estimated by projecting the crown area of all trees of the same species vertically onto the forest floor. This was done within 314-m<sup>2</sup> plots for the climax stage and 28-m<sup>2</sup> plots for the pioneer stage. The study period extended from mid-June to the end of August, 1985. Measurements were taken between 10:00 and 14:00 EST to obviate variations in solar radiation due to the rapidly changing angle of the sun occurring early in the morning and in the late afternoon. No measurements were made during periods of rain.

Spectral irradiance on the forest floor was measured between 15 and 30 cm above ground (1) beneath the pioneer and climax

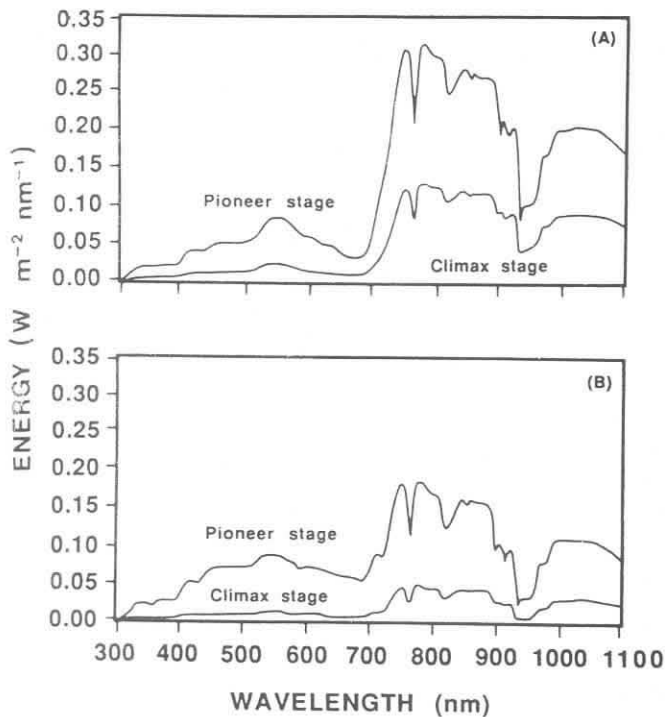


FIG. 1. Quantitative differences in spectral irradiance measured on the forest floor between the pioneer and climax stages on (A) sunny days and (B) cloudy days. An analysis of variance was performed every 5 nm between 300 and 1100 nm. Values are statistically different ( $P < 0.05$ ) at all wavelengths.

stages of the birch – beech – sugar maple stands, (2) on 10 sites of approximately 100 m<sup>2</sup> under a pure concentration of 5 to 10 trees for each species of mature yellow birch, American beech, and sugar maple, and (3) on more than 10 sites of roughly 9 m<sup>2</sup> under a pure concentration of 3 to 5 trees for each species of 5-year-old pin cherry, mountain maple, and red maple. The subcanopy vegetation under the climax stage was very scarce and did not contribute significantly to the light reduction measured. The subcanopy vegetation under the pioneer stage, however, was more abundant and contributed to part of the light reduction measured. Between 13 and 41 repetitions were made under full shade (sunflecks excluded) for each category of canopies on both sunny days (clear solar disk) and cloudy days (obscured solar disk). Light measurements were made only where there was complete crown closure. Great care was taken to ensure that most of the light measured in experiments 2 and 3, above, was transmitted through the canopy of only one species. To do this, measurements were taken in an area on the forest floor with the solar disk in the center of the crown of the concentration of trees of the same species. Seven and 11 repetitions were made in a nearby open field to estimate above-canopy values on sunny and cloudy days, respectively. Spectral irradiance was measured with a LI-1800 spectroradiometer (Li-Cor, Inc., Lincoln, NE) from 300 to 1100 nm at 5-nm intervals (181 measurements).

We assume that shade leaves are predominant in mature species growing in mature stands, whereas sun leaves are predominant in 5-year-old species growing in 5-year-old clearing stands. Therefore, transmittance of shade leaves of yellow birch, American beech, and sugar maple trees in the climax stage, and sun leaves of pin cherry, mountain maple, and red maple trees in the pioneer stage was measured. Shade leaves of the mature species were taken from branches in the lower part of the crown, whereas sun leaves of 5-year-old species were taken from branches in the upper part of the crown. Leaves from branches cut less than 10 min before being measured were used, since we found no difference between the transmittance spectra of freshly detached leaves and those of leaves

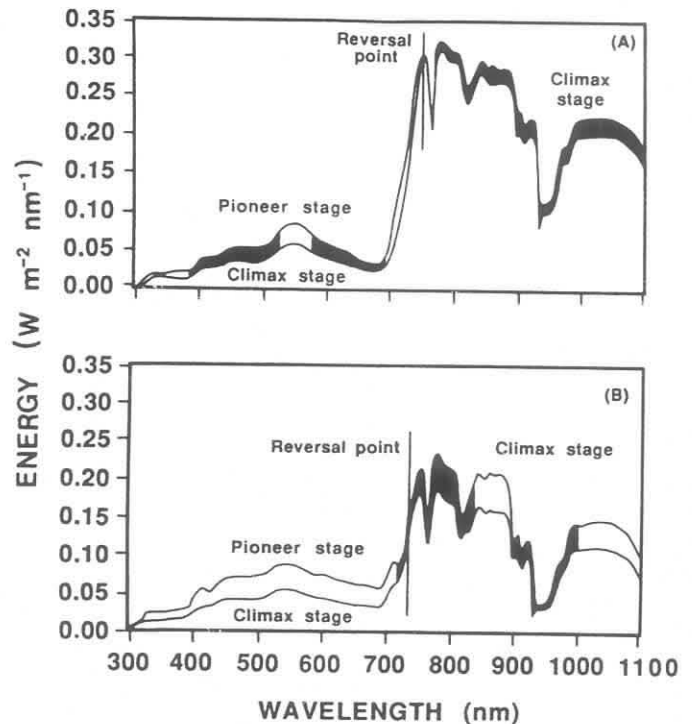


FIG. 2. Qualitative differences in spectral irradiance measured on the forest floor between the pioneer and climax stages on (A) sunny days and (B) cloudy days. The areas under the curves of the climax stage have been multiplied by 2.5 for sunny days and 4.8 for cloudy days to eliminate the quantitative differences found between the two curves. The energy values on the Y-axis are for the pioneer stage only. An analysis of variance was performed every 5 nm between 300 and 1100 nm. Wavelengths between curves where no significant statistical differences occur ( $P > 0.05$ ) are shaded.

still attached to trees. From 18 to 22 leaves, each on a different tree, were measured for each species.

The ratio of transmitted energy to the incident energy was measured between 390 and 1100 nm at 5-nm intervals (143 measurements) on the upper leaf surface with the LI-1800-12 integrating sphere coupled to the LI-1800 spectroradiometer. A glass halogen lamp (General Electric No. 787, 6 V, 10 W) was used as the reference radiation source.

Data were transferred into an Apple III microcomputer for analysis with SPECTRON, a software package designed by the second author. An analysis of variance for two groups was performed for each wavelength measured (143 analyses for transmittance curves and 181 analyses for spectral irradiance curves) ( $P < 0.05$ ).

## Results and discussion

### *Spectral irradiance beneath the pioneer and climax stages*

The pioneer stage transmits significantly ( $P < 0.05$ ) more energy in all wave bands between 300 and 1100 nm than the climax stage on both sunny and cloudy days (Fig. 1; Table 2). On sunny days, the pioneer stage transmits 2.5 times more total energy (between 300 and 1100 nm) than the climax stage, and 4.8 times more on cloudy days. For PAR the differences are even greater, reaching 3.6 on sunny days and 8.3 on cloudy days. This greater discrepancy between the two stages of succession on cloudy days compared with sunny days shows that a greater proportion of diffuse radiation penetrates through gaps under the pioneer stage. The pioneer stage has a more open canopy than the climax stage due to the very irregular vertical structure (i.e.,

TABLE 2. Spectral irradiance (in W/m<sup>2</sup>) above and below the canopy in pioneer and climax stages of the birch – beech – sugar maple stand

	UV (300–400 nm)	PAR (400–700 nm)	FR (700–800 nm)	NIR (800–1100 nm)	Total (300–1100 nm)	BAP <sup>a</sup> (300–500 nm)	R:FR <sup>b</sup> ratio
Sunny days							
Below pioneer stages							
Avg.	1.77	15.97	23.65	61.98	103.37	6.39	0.17
CV (%) <sup>c</sup>	55	47	24	23	27	54	47
Ratio (%) <sup>d</sup>	5.1	4.0	21.3	29.5	13.7	4.1	
Below climax stages							
Avg.	0.46	4.42	9.06	27.05	40.96	1.74	0.14
CV (%)	78	90	20	16	26	94	71
Ratio (%)	1.3	1.1	8.2	12.9	5.4	1.2	
Above canopy							
Avg.	34.98	400.07	111.08	209.76	755.98	155.98	1.16
CV (%)	7	6	7	8	7	7	3
Cloudy days							
Below pioneer stage							
Avg.	2.02	20.55	14.24	32.63	69.43	8.26	0.50
CV (%)	53	52	30	27	36	54	24
Ratio (%)	24.9	31.5	73.5	91.1	54.0	27.0	
Below climax stages							
Avg.	0.23	2.48	3.21	8.63	14.55	0.98	0.32
CV (%)	70	63	45	46	49	66	28
Ratio	2.8	3.8	16.6	24.1	11.3	3.2	
Above canopy							
Avg.	8.10	65.24	19.37	35.83	128.54	30.62	1.11
CV (%)	47	37	36	40	39	42	6

<sup>a</sup>Blue-absorbing photoreceptor acting between 300 and 500 nm (Smith 1982).<sup>b</sup>Ratio between the spectral irradiance at 660 and 730 nm (the absorption maxima of phytochrome) measured with a band width of 10 nm (Smith 1982).<sup>c</sup>Coefficient of variation.<sup>d</sup>Ratio of energy measured below the canopy to that measured above the canopy.

trees varying in heights from 1 to 3 m) of its canopy. In Fig. 2, the areas under the curves of the climax stage have been multiplied by 2.5 for sunny days and 4.8 for cloudy days to make them equal to the areas under the curves of the pioneer stage. Such transformations eliminate quantitative differences, without affecting ratios between wavelengths, and therefore allow one to look at the qualitative variations in spectral irradiance between canopies. It appears after these transformations, that the pioneer stage transmits proportionally ( $P < 0.05$ ) more energy between 300–380, 530–575, and 695–730 nm than the climax stage on sunny days (Fig. 2A), whereas on cloudy days the pioneer stage transmits proportionally ( $P < 0.05$ ) more between 300–720 nm and less between 840–890 nm and beyond 1005 nm than the climax stage (Fig. 2B). The R:FR ratios differ more on cloudy days between the two stages of succession than on sunny days (Table 2).

Both pioneer and climax stages transmit proportionally more energy for each wave band on cloudy days than on sunny days (Table 2). This agrees with the findings of Federer and Tanner (1966), Vézina and Boulter (1966), and Stoutjesdijk (1972a). However, sunflecks were not measured on sunny days, and this may account for the differences measured between sunny and cloudy days, as discussed in Hughes *et al.* (1985).

The changes in spectral energy distribution of solar radiation induced by the deciduous canopies were expected and agreed with previously published data (Freyman 1968; Stoutjesdijk 1972a, 1972b; Goodfellow and Barkham 1974; Floyd *et al.* 1978; Sasaki and Mori 1981). The virtually

identical R:FR ratios found above canopies on sunny and cloudy days (Table 2) agree with the results reported by Holmes and Smith (1977). The average value in PAR found beneath the climax stage on sunny days (4.42 W/m<sup>2</sup>) was comparable with the value reported by Floyd *et al.* (1978), taken under similar conditions, for a mature stand of deciduous trees (5.34 W/m<sup>2</sup>).

#### Spectral irradiance beneath canopies of individual species

Among mature species, yellow birch transmits significantly ( $P < 0.05$ ) more energy than sugar maple and American beech regardless of the sky conditions in some UV and PAR wavelengths, whereas sugar maple transmits significantly ( $P < 0.05$ ) more than American beech on cloudy days in some UV, PAR, and FR wavelengths (Table 3; Fig. 3). Among 5-year-old species, mountain maple transmits significantly ( $P < 0.05$ ) more energy than red maple on sunny days in some wavelengths of PAR and in FR and NIR, while pin cherry transmits significantly ( $P < 0.05$ ) more energy than the other two species on cloudy days in all wave bands (Table 3; Fig. 3). These transmission values generally agree, according to the shade tolerance tables produced by Baker (1949) and Spurr and Barnes (1980), with Horn (1971) who stated that the most tolerant species cast the deepest shade.

Interestingly enough, the absolute amount of PAR measured under full shade (sunflecks excluded) is higher on cloudy days than on sunny days for yellow birch (+47%), pin cherry (+78%), mountain maple (+13%), and red maple (+40%) (Table 3). This comparison does not take

TABLE 3. Spectral irradiance (in W/m<sup>2</sup>) below the canopy of individual species

	UV (300–400 nm)	PAR (400–700 nm)	FR (700–800 nm)	NIR (800–1100 nm)	Total (300–1100 nm)	BAP <sup>a</sup> (300–500 nm)	R:FR <sup>b</sup> ratio
Climax stage							
Sunny days							
American beech	0.31	2.78	8.41	26.25	37.75	1.09	0.10
Yellow birch	0.62	4.87	10.23	30.45	46.27	2.04	0.13
Sugar maple	0.37	3.23	9.47	28.47	41.90	1.27	0.10
Cloudy days							
American beech	0.21	2.32	3.17	8.89	14.58	0.89	0.32
Yellow birch	0.69	7.14	6.30	16.49	30.59	2.89	0.46
Sugar maple	0.30	3.16	3.63	9.85	16.94	1.26	0.32
Pioneer stage							
Sunny days							
Pin cherry	2.23	14.07	21.62	58.27	96.18	6.84	0.15
Mountain maple	1.66	12.82	23.10	62.52	100.91	5.41	0.15
Red maple	1.52	9.34	18.59	52.27	81.73	4.55	0.12
Cloudy days							
Pin cherry	2.56	25.10	16.00	35.22	78.88	10.43	0.47
Mountain maple	1.45	14.50	11.02	26.39	53.36	5.93	0.48
Red maple	1.36	13.05	9.88	23.29	47.60	5.39	0.46

<sup>a</sup>Blue-absorbing photoreceptor acting between 300 and 500 nm (Smith 1982).

<sup>b</sup>Ratio between the spectral irradiance at 660 and 730 nm (the absorption maxima of phytochrome) measured with a band width of 10 nm (Smith 1982).

into account the input of sunflecks on sunny days as we were careful not to include them. However, although some studies have shown that sunflecks often account for more than 50% of the total energy reaching the forest floor of mature stands (Evans 1956; Sasaki and Mori 1981), a recent study done by Weber *et al.* (1985) has shown that the high spots of energy present under canopies on sunny days (i.e., sunflecks) do not contribute significantly more than the diffuse light (i.e., shade light) to the net assimilation of sugar maple seedlings. Furthermore, when Young and Smith (1983) measured an understory herb, *Arnica latifolia*, it was found to have greater carbon gain, less transpiration, and better water use efficiency on cloudy days than sunny days. Considering the latter two studies and the greater amount of PAR measured in this study in full shade under some species on cloudy days compared with sunny days, cloudy days are likely to be more profitable than sunny days for the growth of some understory species.

The R:FR ratios vary among species (Table 3). Yellow birch, for instance, induces a greater R:FR ratio than American beech and sugar maple on both sunny and cloudy days, although the differences are slightly greater on cloudy days. Conversely, R:FR ratios do not vary much among 5-year-old species, particularly on cloudy days. Furthermore, the R:FR ratios measured beneath yellow birch on cloudy days, and to a lesser extent on sunny days, are almost identical to those found beneath 5-year-old species under similar sky conditions.

Morgan and Smith (1981) have summarized the findings regarding R:FR ratios measured beneath different broadleaf deciduous canopies. According to them, with a clear sky (similar to sunny days in this study) R:FR ratios vary from 0.08 to 0.28, while for overcast conditions (similar to cloudy days in this study) they vary from 0.21 to 0.97. The average R:FR ratios reported in Table 3 fit well within these ranges, varying from 0.10 to 0.15 on sunny days and 0.32 to 0.48 on cloudy days.

#### Leaf transmittance

Shade leaves of yellow birch transmit significantly ( $P < 0.05$ ) more PAR than those of American beech (20%) and sugar maple (17%) (Figs. 4 and 5; Table 4). These data correspond well with the differences in canopy transmission in PAR found between yellow birch and both sugar maple and American beech (Table 3). However, the differences in total energy (390 to 1100 nm) transmitted by shade leaves among mature species (Table 4) do not correspond well with the differences in canopy transmission between 300 and 1100 nm recorded on the forest floor among these same species (Table 3).

Sun leaves of 5-year-old mountain maple transmit significantly ( $P < 0.05$ ) more energy in some wavelengths of PAR than those of pin cherry (17%) and red maple (17%), whereas sun leaves of red maple transmit significantly ( $P < 0.05$ ) less in some wavelengths of FR and in NIR than those of pin cherry and mountain maple (Figs. 4 and 5; Table 4). The differences in total energy (390 to 1100 nm) and in PAR (400 to 700 nm) transmitted by sun leaves for each species (Table 4) do not correspond well with the differences in canopy transmission between 300 and 1100 nm and between 400 and 700 nm measured on the forest floor among these same species (Table 3).

In conclusion, leaf transmittance alone does not explain the differences in canopy transmission among the species investigated in this study. Other factors not investigated such as canopy structure and (or) leaf area are obviously important. Finally, shade leaves of mature species transmit, on average, slightly less energy in PAR and more in UV, FR, and NIR than sun leaves of 5-year-old species (Table 4).

#### Ecological significance

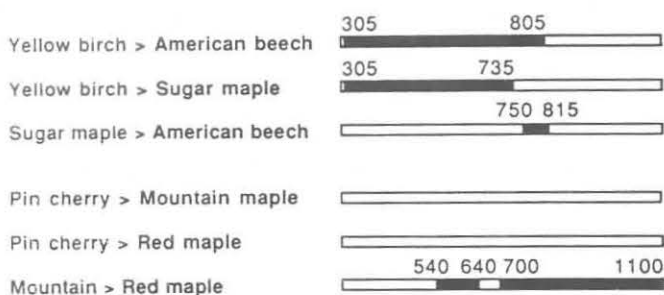
Low R:FR ratios such as those induced by plant canopies have been shown to affect the growth and development of herbaceous and agricultural plants (Morgan and Smith 1981; Hoddinott and Hall 1982; Holmes *et al.* 1982; Corre 1983),

TABLE 4. Transmittance of shade leaves of mature species and sun leaves of 5-year-old species

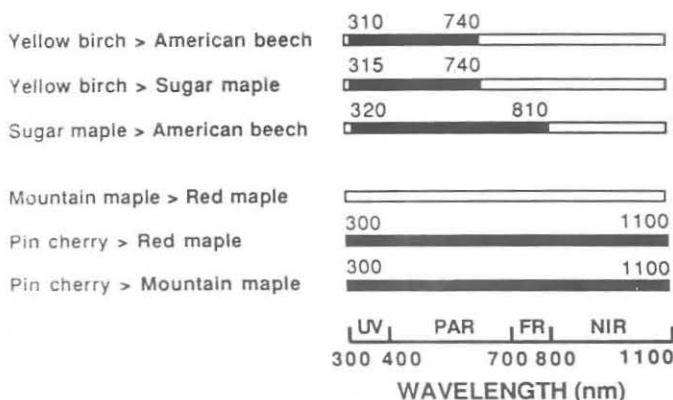
	UV (390–400 nm)	PAR (400–700 nm)	FR (700–800 nm)	NIR (800–1100 nm)	Total (390–1100 nm)
Mature trees (climax stage)					
Yellow birch	0.010	0.076	0.480	0.537	0.327
American beech	0.009	0.061	0.478	0.550	0.326
Sugar maple	0.006	0.063	0.493	0.566	0.335
Average <sup>a</sup>	0.008	0.067	0.484	0.551	0.329
5-year-old trees (pioneer stage)					
Mountain maple	0.004	0.095	0.481	0.536	0.334
Pin cherry	0.002	0.079	0.466	0.533	0.324
Red maple	0.004	0.079	0.451	0.512	0.313
Average	0.003	0.084	0.466	0.527	0.324

<sup>a</sup> Average of the three species for each group.

## SUNNY DAYS



## CLOUDY DAYS

FIG. 3. Significant statistical differences ( $P < 0.05$ ), indicated by the black bars, in spectral irradiance found on the forest floor between different species on sunny and cloudy days. An analysis of variance was performed every 5 nm between 300 and 1100 nm.

*Pinus thunbergii* and *Betula platyphylla* var. *japonica* (Morikawa and Asakawa 1976), *Pinus radiata* D. Don (Morgan *et al.* 1983), and two tropical tree species (Kwesiga and Grace 1986). In this latter study, Kwesiga and Grace (1986) found that the light-demanding species was more sensitive to a decrease in the R:FR ratio than the shade-tolerant species. Based on the studies cited above, the low R:FR ratios induced underneath the early and late successional stages of a birch-beech-sugar maple stand on sunny and cloudy days (Tables 2 and 3) are likely to be of ecological significance for the plants growing underneath. However, our present level of knowledge does not allow us to determine whether or not the differences in R:FR ratios found

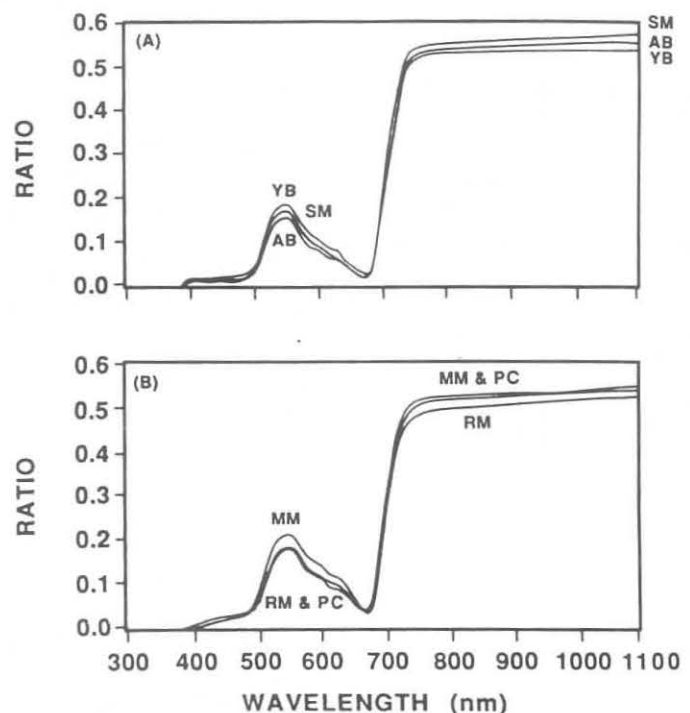


FIG. 4. Comparisons of transmittance of (A) shade leaves of mature yellow birch (YB), American beech (AB), and sugar maple (SM), and (B) sun leaves of 5-year-old pin cherry (PC), mountain maple (MM), and red maple (RM).

between and within the two stages of succession and between sunny and cloudy days (Tables 2 and 3) are of ecological significance.

The function and significance of the BAP in higher plants is fragmentary and equivocal, but it is believed to influence such important plant processes as phototropism, growth, anthocyanin formation, and enzyme activity (Thomas 1981). The variations in BAP reported in Tables 2 and 3 may, therefore, be significant.

PAR comprises the most important wavelengths for plant growth, because it is directly involved in photosynthesis. It is well known that the decrease in PAR caused by forest canopies restricts the growth of many seedlings. Consequently, the quantitative differences in PAR found between and within the two stages of succession and between sunny and cloudy days (Tables 2 and 3) are certainly of ecological

significance for the plants growing underneath. However, there are very few studies on how natural variations in the amount of PAR in birch – beech – sugar maple stands could alter the growth of trees and shrubs. Bellefleur and LaRocque (1983) compared the growth of different seedlings in birch – beech – sugar maple stands between full sunlight and moderately shaded conditions, but no comparison was made between different shaded conditions and only net radiation was measured. Other experiments have been undertaken to evaluate the effects of different PAR values on trees growing in birch – beech – sugar maple stands (Gordon 1969; Logan 1965; Tubbs 1969; Loach 1970), but they all used artificial shade (with a R:FR ratio of approximately 1.2) without any consideration of the low R:FR ratios (between 0.1 to 0.7) normally induced by forest canopies. Therefore, additional research should be undertaken to study the effects of variations in PAR on plant growth with respect to the natural decrease in the R:FR ratio induced by forest canopies.

Based on the shade tolerance tables produced by Baker (1949) and Spurr and Barnes (1980), PAR measured beneath yellow birch among mature trees and beneath pin cherry among 5-year-old trees seems to be more suitable to perpetuate their own species than PAR measured beneath the other species (Table 3). This is because yellow birch is considered less shade tolerant than sugar maple and American beech (Baker 1949; Spurr and Barnes 1980) and pin cherry is less shade tolerant than red maple (Spurr and Barnes 1980). Furthermore, our data show that sugar maple transmits slightly, but significantly ( $P < 0.05$ ), more energy in PAR than American beech on cloudy days (Table 3; Fig. 3), while there is virtually no difference in the R:FR ratio between them. These results do not seem to explain a current ecological hypothesis that sugar maple reproduces preferentially (Woods 1979) and grows better (Cypher and Boucher 1982) under American beech canopies and vice versa.

In summary, it is clear that both the amount of energy between 300 and 1100 nm and the R:FR ratio vary between the pioneer and climax stages, among the species within each stage of succession, and between sunny and cloudy days. Leaf transmittance varies among species but this alone does not explain the differences in the quantity and quality of light reaching the forest floor among these same species. We believe, from experiments with herbaceous and agricultural plants and some forest tree species, that these differences in both light quantity and quality are of ecological significance for the plants growing under birch – beech – sugar maple stands. Finally, based on the knowledge accumulated so far on both the effects of the R:FR ratio on plant growth and the modification of this ratio by forest canopies, the measurement of light quantity (e.g., PAR) alone, as currently used in forestry, is not fully satisfactory to characterize the light conditions under different forest ecosystems.

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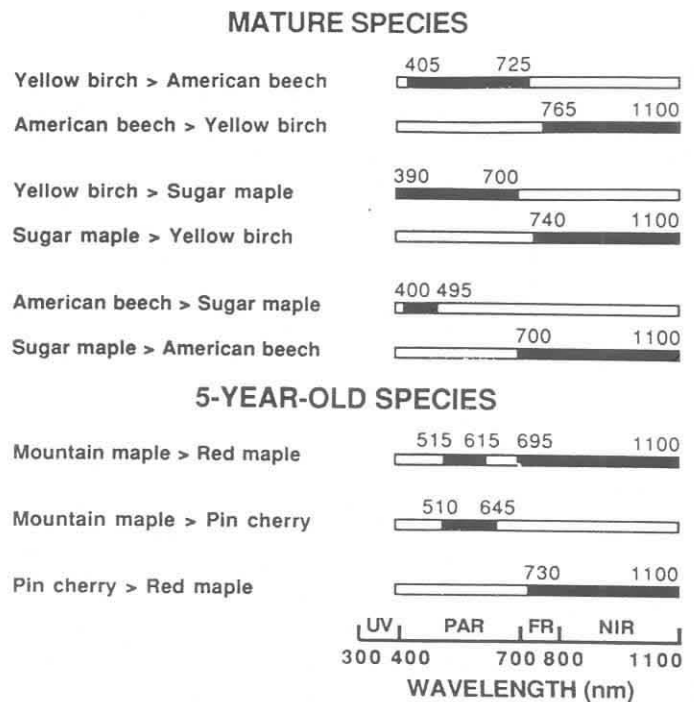


FIG. 5. Significant statistical differences ( $P < 0.05$ ), indicated by the black bars, in leaf transmittance between shade leaves of mature species, and between sun leaves of 5-year-old species (see Fig. 4 for leaf transmittance curves). An analysis of variance was performed every 5 nm between 390 and 1100 nm.

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